A TAXONOMIC REVISION OF PODOCARPUS

I. THE SECTIONS OF THE GENUS AND THEIR SUBDIVISONS WITH SPECIAL REFERENCE TO LEAF ANATOMY

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THIS STUDY of the genus *Podocarpus* stems from a preliminary examination of leaf anatomy. The accounts of Bertrand (1) and Mahlert (10) have yielded conflicting data which seem, after examination of numerous specimens, to be due to the use of material by earlier investigators that had been erroneously identified and to the meagre number of specimens available. With certain corrections, the work of Mahlert (10) appears to furnish a fairly consistent key to the limited number of species considered. Therefore, we began to apply these keys, as corrected, to the species more recently described. We were also inspired by the detailed work of Florin (5) which is confined almost entirely to cuticular anatomy and it seemed that this, in combination with the entire leaf structure, might contribute to a much more accurate classification of species.

Immediately the problem of correctly identifying the specimens found in American collections became a necessity. We have been successful in locating types, isotypes, topotypes and other authentic material of nearly all American species. These provided a sound basis for the comparison of the large number of specimens we had available. All other taxonomic characters shown by the specimens were studied as well and thus it has been possible to render more nearly complete descriptions for many species as well as descriptions of numerous new species and varieties. Hence we are combining the results of our researches on leaf anatomy with the form of presentation used in taxonomic monographs. There is still the shortcoming of having our studies based too largely upon specimens found in American collections, but we have in many instances secured leaf specimens from types and isotypes in European collections and other critically authenticated material, and are therefore enabled to extend our studies and treatment provisionally to collections found in all parts of the world.

A detailed study of leaf anatomy of *Podocarpus* from specimens found in English and Scottish herbaria was made by Orr (11) to determine the value, if any, of these characters in the identification of species. In general our results are in agreement. Unfortunately, in cases of difference, we cannot correlate Orr's work with ours as he does not list the specimens which he examined, and we found the percentage of erroneously named specimens in all herbaria to be extremely high.

Keys based upon leaf anatomy alone lead to all the sections of this large genus. A few individual species may be singled out through leaf anatomy and groups within the sections may also often be recognized by this method. The remaining bulk of the species, then, must ultimately be separated by the usual taxonomic comparison of leaf size and shape, midrib and surface, bud scales, and finally the all-important reproductive characters. Whereas Pilger's keys (12) require a knowledge of reproductive structures at the beginning of analysis of most groups of species, our keys require these details only toward the end of this procedure or in the final determination of species. We feel convinced that our keys to sections and groups of species within sections are very useful due to the abundance of sterile material, and that some of these leaf characters are as important in the definition of sections as the reproductive features which originally formed the entire basis of classification.

DESCRIPTION OF LEAF ANATOMY OF PODOCARPUS

The constancy of internal leaf characters must be demonstrated in the same manner as external characters before they can be used in the determination of groups or species. In using herbarium specimens it must be recognized that methods of collecting and preparing the specimens will alter the color of the leaves, appearance of veins and margins, etc. Mature leaves of the coriaceus type with sufficient sclerids to reinforce the tissues will show a more true character than thin or immature leaves with undeveloped sclerids and cuticle. The internal anatomy of a leaf, easily observed in *Podocarpus* in leaf cross sections, is not changed by collecting methods except in the degree of crushing. But in no case has a thorough study been made of geographical influences on *Podocarpus* and only one or two species (Griffin 8) have been studied in detail in relation to the age of the leaves or the age of the tree or shrub from which the collections were made. Here reference must be made to work on other conifer leaves. An excellent example of such a study is that made by Fulling (7) in *Abies*, and his analysis showed no structural deviations in anatomical features due to sunny or shady portions of a tree, upper or lower portions of a tree, and no correlation with environment. There was only slight variation in positions of resin canals and thickness of hypodermal cell walls, and greater variation in the continuity and abundance of hypoderm. In herbarium specimens he found that the character of the midrib, if at all variable, was practically useless.

A thorough study of leaves from every herbarium specimen of *Podocarpus* available has shown the degree of variation within the species to be small. It has also shown that a single character, such as a large number of vascular sclerids, may be a consistent and distinguishing character in one species or group, while in another species or group it is a character of considerable variation. An analysis of useful anatomical and some external characters follows.

Size of leaf: When a description is based on a single specimen, the variation allowed in the leaves may be entirely inadequate for identification of further specimens. In general, leaves on fruiting branches are smaller, often by half, than other foliage leaves. Extremely large leaves have been collected from seedlings and vigorous shoots of most species.

Midvein: The character of the midvein — prominent or impressed — has been used by taxonomists in species descriptions as a means of differentiation and this procedure has been followed by those identifying herbarium specimens. After careful examination of many leaves in cross section it has been found that it is most valuable when leaves are mature and coriaceous or contain abundant sclerenchyma. The very strict selection of sulcate or prominently ribbed leaves has led to errors in identification in species where it is a variable character, and a number of errors have been made by ignoring the character entirely.

Vascular bundle: The shape is often characteristic in the sections, but little difference among species within the sections has been observed. Figs. 1–5 showing leaf sections include extremes in bundle size and shape.

Transfusion tissue: Transfusion tissue is located on each side of the vascular bundle in a wing formation. It may be a small area (figs. 1 & 7) in sections *Dacrycarpus* and *Stachycarpus*, larger and clear in sections *Sundacarpus* (fig. 2) and *Eupodocarpus* or extend halfway into the blade of the leaf in sections *Afrocarpus* (fig. 3) and *Polypodiopsis* (fig. 4).

Resin canals: Basically there is always one resin canal directly below the vascular bundle. In sections *Sundacarpus*, *Afrocarpus*, *Polypodiopsis* and *Eupodocarpus* (African) it may be flanked by an additional canal on each side. Always in African *Eupodocarpus* (fig. 5) and often in *P. Rospigliosii* (*Polypodiopsis*) there are also resin canals in the extreme margins of the leaves. A special deviation from this pattern will be described under *P. Rospigliosii*.

Accessory transfusion tissue: This tissue has often been described in the literature as, among the Coniferae, it is peculiar to certain sections of *Podocarpus*. It consists of pitted sclerids arranged perpendicular to the vascular bundle in a layer varying in thickness and degree of thickening, extending from each side of the transfusion tissue into the margin of the leaf. This tissue may be entirely absent or replaced by isolated sclerids. Figures 2, 3, 5, 8 and 9 show accessory transfusion tissue. The nature of this tissue has been ably discussed by Worsdell (16) and Orr (11).

Hypoderm: Many previous workers have endeavored to use the size of hypodermal cells, thickness of walls, size of cell lumen, continuity of the layer, number of layers, and length of interruptions in the layers as differentiating characters. We also recognize and use the appearance of the hypoderm, but great care must be observed to state its limitations as many species show it to be variable in one way or another instead of being constant. We believe that variation, when limits are stated, does not detract from its use in indentification. Hypoderm may be seen in figs. 1, 3, 4, 5, 8, 9 and 10.

Sclerids: We now refer to types of sclerids present in the leaves other than those already described as forming distinct tissues.

a. VASCULAR SCLERIDS: Associated with the vascular bundle there are often long fibres with thick walls and almost no lumen. Measurements have shown these to be over a millimeter in length in some cases. They may be scattered around the bundle, only above or below the bundle, arranged as a heavy layer above the bundle or as two small groups on either side of the resin canal. Variation seems to be caused by age of tree and position of the leaf on the tree.

Similar fibres of extreme length and closed lumen are often scattered between hypoderm and palisade on the upper side, or in addition to hypoderm between stomatal rows on lower side, but never form a distinct layer and are very rarely located at margins.

b. AUXILIARY SCLERIDS: In some species palisade cells are altered into pitted, thickened sclerids as shown in fig. 9. They are usually, but not always, much enlarged and the lumen remains large. Mesophyll cells are also sclerified in some species and are distinguished from the palisade sclerids by their position parallel to the cross section of the leaf blade and perpendicular to the palisade; and from the accessory transfusion tissue by their larger size and being shorter and wider. They may form a distinct layer between palisade and accessory transfusion tissue or they may be merely isolated.

Palisade: Except in cases where the palisade consists of two or three layers and shows this thickness consistently, this tissue cannot be used in identifying herbarium specimens. It is altered by light, moisture and age of leaf.

Stomata: Leaves are said to be hypostomatic when stomata are found only on one side (normally abaxially), amphistomatic when they are found on both sides. The latter may be further qualified when more stomata are to be found on one side than the other. Usually arranged longitudinally in rows, the number of rows is a function of the width of the leaf and varies accordingly. The rows may be crowded so as to be scarcely distinguishable, or they may be separated by several rows of ordinary epidermal cells. The subsidiary cell pattern of the stoma was considered in detail by Florin (5). Guard cells are flanked by two to four laterally adjacent and two polar cells and there may be a second rank or partial rank of such cells.

Cuticle: The thickness of the cuticle is an extremely variable character and there is not enough information concerning habitat available on herbarium specimens for correlation with cuticular thickness for this character to be useful except in very special cases.

In the cells of the first rank encircling the stoma, there may be a special furrow in the cuticular thickening forming a complete translucent ring. This was described by Florin (5) and we refer to this character as the Florin ring (compare figs. 11 and 12). Within section *Eupodocarpus* this

character is diagnostic in separating subsections A, C and D from subsection B. It may be present or absent in other sections where the character has been disregarded.

MATERIAL AND METHODS

The method for examination of cross sections of leaves of herbarium specimens of *Podocarpus* is quite simple. The leaf (more than one from different parts of twig or tree if abundant material is available) is soaked in distilled water until it sinks to the bottom of the vial. Then the leaf, or 1–2 cm. lengths from the midportion and base are placed in a split 3 cm.-length of elder pith. The sections are cut by hand with the *new* edge of a safety-razor blade and transferred to 50% glycerine. They may be examined in about an hour or, by evaporating out the water, permanent mounts may be made in glycerine jelly or the sections may be stored in vials in the pure glycerine. No staining of cross sections is necessary for any of the observations made in this paper.

To observe the epidermis, a 3–8 mm. section from the midportion of the leaf is macerated enough to separate the epidermis from the other tissues. The acid is washed out and it is then stained in a 50% solution of safranin. The stained epidermis is cleared and mounted in balsam. Thus the pattern of subsidiary cells of stomates and the Florin ring (fig. 11) as well as epidermal cell arrangement can be seen clearly.

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We wish to express our appreciation of the kind cooperation of the curators of herbaria listed below for loans of most specimens in American collections. Herbaria whose collections were studied are cited by employing the following symbols to conform with those given by Lanjouw (9): Academy of Natural Sciences of Philadelphia (Ph), Arnold Arboretum (A), Bishop Museum at Honolulu (Bish), University of California at Berkeley (UC) and Los Angeles (LA), California Academy of Science (CAS), Chicago Natural History Museum (Field Museum) (F), Cornell University (CU), University of Illinois Herbarium (Ill), University of Michigan (Mich), Gray Herbarium (GH), Missouri Botanical Garden (Mo), New York Botanical Garden (NY), University of Tennessee (Tenn), Rutgers University Herbarium (NJU), Stanford University

Dudley Herbarium (DS), United States National Herbarium (US), National Herbarium of Venezuela (Ven), Yale University Herbarium (YU), and Yale Forestry School (Y).

Podocarpus L'Heritier ex Persoon, Syn. 2: 580. 1807, *nomen conservandum*; Endlicher, Gen. Pl. 262, no. 1800. 1837, Syn. Conif. 206. 1847; L. C. & A. Richard, Comm. Bot. Conif. 124. 1826; Blume, Enum. Pl. Javae 1: 88. 1827; Bennett in Horsfield, Pl. Jav. Rar. 35. 1838; Carrière, Traité Conif. ed. 2, 643. 1867; Parlatore in DC. Prodr. 16(2): 507. 1868; Gordon, Pinetum ed. 2, 326. 1875; Bentham & Hooker f., Gen. Pl. 3: 434. 1880; Eichler in Nat. Pflanzenfam. II. 1: 104. 1889; Beissner, Handb. Nadelholzk. 193. 1891; Pilger in Pflanzenreich IV. 5(Heft 18): 54. 1903, in Nat. Pflanzenfam. Nachtr. III, 4. 1906, and ed. 2, 13: 240. 1926; Florin in Svenska Vet.-Akad. Handl. ser. 3, 10(1): 262. 1931, 19(2): 8. 1940, in Palaeontographica 85(B7): 577. 1944; Wasscher in Blumea 4: 360. 1941.

Nageia Gaertner, Fruct. Sem. 191. 1788, in part, description confused, *nomen rejiciendum*; O. Kuntze, Rev. Gen. 2: 789. 1891; Baillon, Hist. Pl. 12: 40. 1892.

Myrica sp. Thunb.; *Taxus* sp. Willd.; *Juniperus* sp. Roxb.

Coniferous trees or shrubs, usually dioecious, with large simple leaves, needle leaves or scale leaves, usually alternate (opposite decussate in section *Polypodiopsis*, sometimes subopposite in section *Nageia* and species of section *Afrocarpus*). Leaves amphistomatic or hypostomatic, with or without hypoderm, with transfusion tissue, with one resin canal always below the phloem of vascular bundle and sometimes additional resin canals between this and leaf margin, and as many as vascular bundles in section *Nageia*. Pollen cones cylindrical, terminal (section *Dacrycarpus*) or spicately arranged on lateral branches (section *Stachycarpus*) clustered on special peduncles or solitary, 1–3 fascicled in axils of leaves. Microsporangia 2 on each sporophyll, abaxial, dehiscing with a slit, usually with a centrally placed apiculus of sporophyll; pollen grains usually with 2 air-bladders or wings (or 3 or more in section *Dacrycarpus*). Ovulate cones terminal on short lateral twigs (sections *Microcarpus* and *Dacrycarpus*), or seldom spicate with separated ovules (section *Stachycarpus*), or with 1–2 ovules borne at or near the end of a special axillary fruiting branch, the strobilar axis beneath the seed remaining woody or becoming swollen fleshy at maturity. Ovules inverted, with micropyle near place of attachment, surrounded by and enclosed in an epimatium fused with seed coat except near micropyle and becoming coriaceous or fleshy with the middle layer of seed coat usually indurated, woody, or stony.

SUBDIVISION OF THE GENUS

The divisions of *Podocarpus* by Pilger in 1926 (13) following Engler (4) appears to us to be inconvenient and not well founded. His subgenera *Stachycarpus* and *Protopodocarpus* are each composed of heterogeneous assemblages of categories some of which appear to be more closely related to sections in the alternative subgenus than to each other. To set up additional subgenera in an effort to re-group them might cause more confusion than to list them all as sections. We agree with Wasscher (14) who states on page 361, "I doubt whether the subdivision into sub-genera is right. Perhaps we had better not distinguish any sub-genera, but only six equivalent groups which might be either sub-genera or sections." Our treatment is therefore in full agreement with Wasscher except that we are

adding two other sections for categories mostly outside of the range covered by his treatise. There is only one difference in sectional names: Wasscher's section *Stachycarpus* included plants which we are now placing in the new section *Sundacarpus*. Florin (5), p. 266, also suggested the advisability of such a revision.

The difference in our treatment of this genus and that of Pilger (13) may best be shown by the following outline:

Pilger (1926)	Present treatment
I. Subgen. Stachycarpus Engl.	
A and Ab	7. Stachycarpus Endl., in part.
B	4. Afrocarpus n. sect. 6. Sundacarpus n. sect.
II. Subgen. Protopodocarpus Engl.	
Sect. 1. Dacrycarpus Endl.	1. Dacrycarpus Endl.
Sect. 2. Microcarpus Pilg.	2. Microcarpus Pilger
Sect. 3. Nageia Endl.	3. Nageia Endl.
A. with swollen receptacle	A. with swollen receptacle
B. with woody receptacle	B. with woody receptacle 5. Polypodiopsis Bertrand
Sect. 4. Eupodocarpus Endl.	8. Eupodocarpus Endl.
A. without bracts beneath receptacle	A. African species. C. Central, S. American spp. D. Chile, SW Pacific spp.
B. with bracts beneath receptacle	B. Asia, S. Pacific, Austr.

KEY TO SECTIONS AND SUBSECTIONS

Leaves small, awl-shaped or scale like, amphistomatic, attached spirally.
  Leaves of awl-shaped spreading needles, triangular or 4-sided in cross-section, with hypoderm, single resin canal; when flat, on pectinate frondose twigs of limited growth, giving the plants dimorphic foliage with the flat leaves compressed in vertical plane, ovule and seed with bract as long as ovule and fully incorporated with epimatium throughout its length; receptacle becoming swollen or fleshy as seed ripens (fig. 1.).....Sect. 1. *Dacrycarpus.*
  Leaves of loosely appressed scales, reddish, seed without fleshy receptacle and with bract shorter than seed, free from seed.....Sect. 2. *Microcarpus.*
Leaves large, not awl-shaped needles or scale leaves.
  Leaves relatively broad with many parallel veins and as many resin canals beneath phloem, with hypoderm.....Sect. 3. *Nageia.*
    Leaves amphistomatic, receptacle of seed becoming swollen and fleshy.....Subsect. *A.*
    Leaves hypostomatic, receptacle of seed remaining woody.....Subsect. *B.*
  Leaves with a single median vein.
    Leaves amphistomatic, without accessory transfusion tissue.
      Leaves alternate, spreading on all sides of twigs, seldom sub-opposite, with hypoderm on both sides, with transfusion tissue spread wing like from vascular bundle but without accessory transfusion tissue (fig. 3).....Sect. 4. *Afrocarpus.*
      Leaves opposite, 4-ranked, decussate, but nevertheless usually spread out in a single plane (fig. 4).....Sect. 5. *Polypodiopsis.*
    Leaves hypostomatic, or prevailingly hypostomatic.
      Leaves without hypoderm.

Leaves large, not distichous, 5–16 cm. long (usually 8–11) and 6–14 mm. broad, with accessory transfusion tissue (fig. 2).....
.....Sect. 6. *Sundacarpus*.
Leaves small, less than 3 cm. long and less than 5 mm. wide, usually spread apart in pectinate branches, (a few Old World species or their seedlings may be amphistomatic) without accessory transfusion tissue (fig. 7).....Sect. 7. *Stachycarpus*.
Leaves with hypoderm or hypodermal fibres, or if hypoderm is scanty, leaves with well developed accessory transfusion tissue, seeds with swollen, fleshy, or leathery receptacle.....Sect. 8. *Eupodocarpus*.
Leaves with 3–5 resin canals, a pair of these near margin of leaf, bracts beneath receptacle absent, Florin ring present in subsidiary cells surrounding stomates (fig. 11).....Subsect. *A*.
Leaves with 1–3 resin canals, all at vascular bundle (figs. 5 & 8).
Bracts present beneath receptacle, Florin ring absent (fig. 12).
.....Subsect. *B*.
Bracts absent beneath receptacle, Florin ring present (fig. 11).
Accessory transfusion tissue well developed (fig. 9).....
.....Subsect. *C*.
Accessory transfusion tissue absent or replaced by sclerids (fig. 10).....Subsect. *D*.

Sect. 1. **Dacrycarpus** Endlicher, Syn. Conif. 221. 1847; Carrière, Traité Conif. ed. 2, 676. 1867; Parlatore in DC. Prodr. 16(2): 520. 1868; Pilger in Pflanzenreich IV. 5(Heft 18): 55. 1903, in Nat. Pflanzenfam. ed. 2, 13: 242, 245. 1926; Florin in Svenska Vet.-Akad. Handl. ser. 3, 10(1): 267, 269. 1931, 19(2): 23, 69. 1940, in Palaeontographica 85(B7): 577. 1944; Wasscher in Blumea 4: 386–88. 1941.

Trees or shrubs with small alternate scale like, awl-shaped or flattened leaves, usually amphistomatic, with hypoderm, single resin canal beneath single midvein; dimorphic foliage may include distichous twigs of determinate growth with vertically flattened doubly falcate leaves appearing among branches with awl-shaped leaves, in these the vascular bundle may appear turned with xylem and resin canal on opposite sides of phloem. Pollen cones cylindrical, terminal on short lateral twigs with long apiculate sporophylls resembling leaves, with 2 sporangia; pollen with 3 or more wings. Ovulate cones terminal on lateral twigs with one or two inverted ovules (usually only one developing into seed) with bract adherent to and as long as ovule, becoming consolidated with epimatium throughout its length, the cone axis and sterile bracts below seeds usually becoming warty and fleshy. Southeastern Asia, East Indies and South Pacific Islands to New Zealand.

Sect. 2. **Microcarpus** Pilger in Pflanzenreich IV. 5(Heft 18): 58. 1903, in Nat. Pflanzenfam. ed. 2, 13: 243–245. 1926; Florin in Svenska Vet.-Akad. Handl. ser. 3, 10(1): 270. 1931, in Palaeontographica 85(B7): 577. 1944.

Sect. *Dacrycarpus* Parlatore in DC. Prodr. 16(2): 520. 1868, in part; Vieillard ex Carrière, Traité Conif. 697. 1867.

Shrubs with small alternate scale like leaves, amphistomatic. Ovulate cones with small single crested ovule, with its bract free and much shorter than ovule or seed, with strobilar axis below seed not fleshy, but seed enclosed in epimatium surrounding stony seed coat. (*Podocarpus ustus* Brongn. & Gris) New Caledonia.

Sect. 3. **Nageia** Endlicher, Syn. Conif. 207. 1847; Carrière, Traité Conif. ed. 2, 635. 1867; Parlatore in DC. Prodr. 16(2): 507. 1868; Pilger in Pflanzenreich IV. 5(Heft 18): 58. 1903, in Nat. Pflanzenfam. ed. 2, 13: 242, 245. 1926; Florin in

Svenska Vet.-Akad. Handl. ser. 3, 10(1): 272, 274. 1931, in Palaeontographica 85(B7): 578. 1944; Wasscher in Blumea 4: 415. 1944.

Trees and shrubs sometimes monoecious but mostly dioecious with leaves broad, having many parallel veins, either amphistomatic or hypostomatic, with resin canals beneath each of the many vascular bundles. Pollen cones cylindrical, single or several-fascicled at the end of an axillary peduncle. Ovulate cone at the terminal portion of an axillary fertile branch, a reduced strobilus whose scaly, many-noded axis may become fleshy or remain woody. Southeastern Asia, East Indies and Philippines to New Guinea.

Sect. 4. **Afrocarpus** sect. nov.

Sect. III *Stachycarpus* Endlicher, Syn. Conif. 218. 1847, in part; Pilger in Pflanzenreich IV. 5(Heft 18): 63. 1903, in part.

Subgen. *Stachycarpus* (Endl.) Engler in Nat. Pflanzenfam. Nachtr. 21. 1897; Pilger in op. cit. ed. 2, 13: 242. 1926, in part; Florin in Svenska Vet.-Akad. Handl. ser. 3, 10: 266. 1931, as "Artgruppe 2."

Arbores vel frutices dioici foliis magnis planis spiraliter dispositis, amphistomaticis, 1-vascularibus, ducto resinifero unico, fibrosis; strobilis masculis cylindricis, axillaribus, solitariis aggregatisve; strobilis foemineis ramulo squamuloso proprio ligneo fultis; ovulis 1–2, anatropis, epimatio carnoso involucratis, a squamula saepius minore liberis; seminibus globulosis vel piriformibus; strato tegumenti medio indurato.

Africa from equatorial region southward. Type of section: *P. falcatus*.

Sect. 5. **Polypodiopsis** Bertrand in Ann. Sci. Nat. ser. 5, 20: 65. 1874; Florin in Svenska Vet.-Akad. Handl. ser. 3, 10(1): 275. 278, pl. 23, 30. 1931, 19(3): 8, 25, 71, pl. 1, 2. 1940, in Palaeontographica 85(B7): 578. 1944; Wasscher in Blumea 4: 423–427. 1941.

Sect. *Nageia* Pilger in Pflanzenreich IV. 5(Heft 18): 58. 1903, in part.

Subgenus *Protopodocarpus* Engler sect. *Nageia* Pilger in Nat. Pflanzenfam. ed. 2, 13: 245. 1926, in part, (B).

Dioecious trees with opposite (4-ranked decussate) foliage. Leaves small, amphistomatic, with single vascular bundle usually flanked by wing like appendages of transfusion tissue (as in *Afrocarpus*), with a resin canal beneath phloem and sometimes several to many other resin canals between center and leaf margin; hypoderm fibres present. Pollen cones cylindrical, 1 — several on the end of a special axillary branch with opposite pairs of scale leaves. Ovulate cone at end of an axillary fruiting branch, bearing terminally a single inverted ovule free from a small subtending bract, epimatium fused with and completely surrounding ovule and seed as part of a fleshy layer, sterile bracts of cone axis below seed scale-like decussate. Seed large, slightly elongated or pear-shaped. South America and South Pacific Islands, New Guinea, New Caledonia and Fiji.

Sect. 6. **Sundacarpus** sect. nov.

Podocarpus sect. 2 *Taxoideae*, Bennett in Horsfield, Pl. Jav. Rar. 40. 1838, in part.

Stachycarpus Endlicher, Syn. Conif. 218. 1847, in part; Pilger in Pflanzenreich IV. 5(Heft 18): 63. 1903, in part.

Subgenus *Stachycarpus* Engler sect. *Nageia* Pilger in Nat. Pflanzenfam. ed. 2, 13: 245. 1926, in part, (B); Wasscher in Blumea 4: 380. 1944, in part.

Arbores dioicae foliis magnis planis spiraliter dispositis; foliis hypostomaticis, hypodermate carentibus, ducto resinifero saepius unico; strobilis masculis cylindricis, axillaribus, apice pedunculi brevis aggregatis; strobilis

foemineis pedunculo constantibus 1–3 ovulis bracteatis donato ad apicem inaequaliter dichotomo, squamulis ab ovulo liberis semper parvis; seminibus anatropis, epimatio carnoso, putamine duro.

East Indies, Philippine Islands, New Guinea, Cape York Peninsula of Australia. Type of section: *Podocarpus amarus* Blume.

Sect. 7. **Stachycarpus** Endl. (emend.), Syn. Conif. 218. 1847, in part; Carrière, Traité Conif. 672. 1867, in part; Parlatore in DC. Prodr. 16(2): 518. 1868, in part; Eichler in Nat. Pflanzenfam. II, 1: 105. 1889, in part; Pilger in Pflanzenreich IV. 5(Heft 18): 63. 1903, in part; Florin, in Svenska Vet.-Akad. Handl. ser. 3, 10(1): 266. 1931, as "Artgruppe 1"; in Palaeontographica 85(B7): 577. 1944, in part.

Prumnopitys Phil. in Linnaea 30: 731. 1860.

Stachycarpus Van Tieghem in Bull. Soc. Bot. France 38: 162. 1891, as genus; Engler in Nat. Pflanzenfam. ed. 1, Nachtr. 21, 1897, as subgenus; Pilger in op. cit. ed. 2, 13: 242. 1926.

Dioecious trees with small spirally arranged leaves spread apart distically in one plane. Leaves of flattened needles usually hypostomatic, without hypoderm, with median vein, with transfusion tissue but without accessory transfusion tissue, a single resin canal beneath phloem. Pollen cones in spicate arrangement on special branches. Ovulate cones consisting of an axis bearing inverted bracted ovules in spicate arrangement on the end of a special fruiting branch of which several or only one may mature as a seed, or in some species only the terminal ovule may develop. Ovule and seed usually covered with soft epimatial layer which may form a distinct crest at the tip farthest from micropyle. Central and South America to New Zealand, Australia and New Caledonia.

Sect. 8. **Eupodocarpus** Endlicher, Syn. Conif. 208. 1847; Bennett in Horsfield, Pl. Jav. Rar. 39. 1838, as sect. 1; Miquel, Fl. Ind. Bat. 2: 1072. 1859; Carrière, Traité Conif. ed. 2, 644. 1867; Parlatore in DC. Prodr. 16(2): 509. 1868; Gordon, Pinetum ed. 2; 326. 1865; Eichler in Nat. Pflanzenfam. II, 1: 104. 1889; Beissner, Handb. Nadelholzk. 193. 1891; Pilger in Pflanzenreich IV. 5(Heft 18): 73. 1903, in Nat. Pflanzenfam. ed. 2, 13: 242, 247. 1926; Foxworthy in Philipp. Jour. Sci. 6: 160. 1911; Stiles in Ann. Bot. 26: 448. 1912; Gibbs in Ann. Bot. 26: 543. 1912; Hickel in Lecomte, Fl. Gén. Indo-Chine 5: 1066, 1931; Florin in Svenska Vet.-Akad. Handl. ser. 3, 10(1): 279, 283. 1931, in Palaeontographica 85(B7): 577. 1944; Wasscher in Blumea 4: 427. 1941.

Trees and shrubs, usually dioecious, with alternate leaves arising from all sides of twigs. Leaves flat, hypostomatic, with hypoderm represented, with 1–5 resin canals, transfusion tissue, and accessory transfusion tissue with exceptions. Pollen cones axillary, single or grouped or variously clustered on peduncles. Ovulate cones borne singly on axillary peduncles bearing 1–2 terminal inverted ovules surrounded by epimatium, their subtending bracts separate and small, usually included in cone axis which, with sterile bracts, become a swollen or a fleshy receptacle. Seeds mostly ovoid or globose, frequently with an apiculus at exposed end, with the stony layer relatively thin. Central and South America, Africa, Asia, Australia, South Pacific Islands.

GEOGRAPHIC DISTRIBUTION

Three large areas of the tropics and southern hemisphere are occupied by species of *Podocarpus*. These are:

I. the area from southern Japan and China, Nepal, Sumatra to Australia including Tasmania and New Zealand, thence northward to the Fiji Islands and the Philippines.

II. South Africa and Madagascar extending northward only a few degrees north of the equator.

III. South and Central America northward almost to the Tropic of Cancer including the West Indies.

These three areas are geographically isolated by large oceanic expanses at the Equator and temperate zones and by the frigid zone in the Antarctic. The Indian Ocean and a gap formed by the peninsular part of India (where there are no conifers) separates I and II; the south Atlantic and Pacific Oceans isolate Area III.

In these three major areas the sections of *Podocarpus* are very unequally represented. Section *Eupodocarpus* is found in all of these areas, but the subsections differ. All other sections occupy either only one or parts of two of these larger areas.

Area I includes parts of seven of the eight sections of the genus which are unequally distributed and only two of the four subsections of *Eupodocarpus* which overlap. Within this region sect. *Microcarpus* is known only from New Caledonia, a relatively small island on which representatives of four other sections are encountered. Sections *Nageia* and subsection B of *Eupodocarpus* range farther northward in this area than species of *Podocarpus* anywhere else in the world, crossing the Tropic of Cancer and extending to about 34° N. latitude. The latter subsection covers almost the entire region of Area I excepting Tasmania and New Zealand. (Some of these plants may be cultivated in similar latitudes in the U. S. even though none of the native American species have spread north of the Tropic of Cancer on the American continent.)

In Area I the range of sect. *Sundacarpus* is restricted to the Sumatra-Philippine Islands-New Guinea triangle, overlapping and almost completely surrounded by the sections, *Nageia* and *Dacrycarpus*. The first two of these are not found east or far south of New Guinea, while section *Dacrycarpus* extends to New Zealand.

Australia has four sections represented, none of which is peculiar to this continent. All of them are extensions of the ranges of sections or subsections with extremely wide distributions. The range of section *Stachycarpus*, which touches northeastern Australia extends across the Pacific to South and Central America. Section *Eupodocarpus* is represented in Australia by two overlapping subsections, B and D. The former (B) ranges to China and Japan, and eastward to the Fiji Islands and New Caledonia, but not to New Zealand nor Tasmania, while the latter (D) ranges eastward across the Pacific from southeastern Australia, Tasmania, New Caledonia and New Zealand to Chile.

In Area II (Africa) only two sections are represented. Section *Afrocarpus* is found nowhere else, while subsection A of *Eupodocarpus*, with a similar distribution, includes Madagascar.

In Area III (America) three sections are represented: *Stachycarpus*, *Polypodiopsis* and subsections C and D of *Eupodocarpus*. All of these excepting C of *Eupodocarpus*, range across the south Pacific — *Polypodiopsis* from Venezuela and Peru to Fiji, New Caledonia and New Guinea; *Stachycarpus* from Venezuela and Costa Rica to New Zealand, New Caledonia and Queensland; subsection D from Chile to New Zealand, Tasmania, New South Wales and New Caledonia.

ORIGIN OF PODOCARPUS

The place of origin of *Podocarpus* would seem to be included in Area I where seven of the eight sections of the genus are represented. The tropics of Area I and well into the North Temperate Zone is a region inhabited by many species of Pinaceae, several Taxodiaceae, *Amentotaxus* and *Cephalotaxus*. Hence, if any single general area of the world may be designated, in which several or all of these families of conifers may have had a common origin, it is here where these diverse conifers still overlap. This is of special interest since their origin may go back to the close of the Paleozoic or not later than the early Mesozoic and it is known that there have been major changes in the continental areas since that time.

The conifers, with seeds as their only method of reproduction (before there were land animals other than amphibians and reptiles to aid in seed dispersal) probably spread very slowly. Their species never became truly world-wide. It may be presumed that some Podocarpaceae still occupy very largely the area or general region of their origin (sections *Nageia*, *Sundacarpus*, *Microcarpus*, *Dacrycarpus* and subsection B of *Eupodocarpus*). *Afrocarpus* and subsection A of *Eupodocarpus* may have migrated westward from Area I over land connections during an early period. Other sections such as *Stachycarpus*, *Polypodiopsis* and subsection D of *Eupodocarpus* have, on the contrary, spread themselves over areas incredibly distant, since they now occupy areas that are very far apart, with barriers of the South Pacific between.

The evolution of Podocarpaceae proceeded throughout the Mesozoic. They spread slowly until birds and mammals appeared, which might aid in the dissemination of their seeds. It must be remembered that conifers, cycads, ginkgos and ferns were the dominant land plants up until the sudden appearance of angiosperms in the Cretaceous.

However, Area II, with section *Afrocarpus* and subsection A of *Eupodocarpus*, is far removed from Area I. These areas must have been connected during the early Mesozoic and likewise Area III, which is separated from II by the Atlantic Ocean. Assuming no barriers, the mere spread of the plants of these sections to these areas must have required a long period of time.

There is evidence in leaf anatomy to indicate that sect. *Polypodiopsis* has characteristics in common with sect. *Afrocarpus* — amphistomatic leaves, well developed transfusion tissue into wing like expansions of the vascular bundle with the lack of accessory transfusion tissue (cf. figs. 3

& 4). There is also some evidence in leaf anatomy indicating that subsection C and subsection A of *Eupodocarpus* have a common origin. This is indicated by the Florin ring (fig. 11) which they (along with D) have in common and by the absence of bracts beneath the receptacle (for these details see key to sections and subsections).

The apparent crossing of the South Pacific is also indicated by other genera in this family — *Dacrydium* with one species in Chile, *Araucaria* with two species in Area III and the remaining species in the southern part of Area I. Furthermore, sect. *Dacrycarpus* had a foothold in Chile during the Tertiary. Florin has demonstrated fossils in Chile that may be referred to this section. There are other conifers that appear to have crossed the South Pacific as well as primitive angiosperms.

These extreme migrations of several sections and their descendants which appear to have spanned several oceans in encircling the globe need not be believed if one accepts some form of the Wegener theory of continental drift. However, the sections of the genus must have been very unevenly distributed with their ranges widely diversified on Gondwana before separation of the continents took place. By using the maps given by DuToit (3, figs. 7 and 12, for example) one may account for the origin and dispersal of sections.

According to this, *Afrocarpus* and *Eupodocarpus* A (in Area II) would have come from or had an origin in common with *Podocarpus* of Area I. *Polypodiopsis* in Area III could have been derived from *Afrocarpus* in Area II and spread via Patagonia to New Caledonia and New Guinea. *Eupodocarpus* C could have come from *Eupodocarpus* A, giving rise, in turn, to *Eupodocarpus* D which reached New Zealand and Australia by the same route. The same holds for *Stachycarpus* except that we find some evidence in leaf anatomy to indicate migration in the opposite direction, from Australia and New Zealand via Patagonia to Central America. *Stachycarpus* may have been derived from *Sundacarpus* to which it is related and which has remained in Area I. The Wegener theory, therefore, serves to clear up many of the problems in the distribution of these and other conifers, to which there is no satisfactory alternative answer.

There is also the question as to which section of *Podocarpus* is most primitive. If the choice lies among the sections included in Area I, with seven sections represented, the selection is narrowed so very little that the decision must still be made on the basis of morphological characters. It is possible that some would contend the section *Eupodocarpus* to be one of the more primitive sections due to its wide distribution over all parts of the southern hemisphere. Our basis of judgment in placing this last is founded upon the almost universal hypostomatic condition of the leaves and the well-developed accessory transfusion tissue (absent through loss in the course of evolution only in sub-section D). On the other hand, sections *Microcarpus* and *Dacrycarpus* include the small awl-shaped or scale leaves now known to be characteristic of primitive conifers (Florin 6). Section *Microcarpus* has the bract separated from the ovule which

would indicate that this section is more primitive than sect. *Dacrycarpus*. The latter may be advanced with respect to fusion of cone scale with the ovuliferous scale, represented by the epimatium, but is otherwise, in common with section *Microcarpus*, primitive in having the strobili borne on the ends of ordinary lateral branches rather than specialized fruiting branches. This is the condition shown by Florin (6) for several fossil conifers from the Paleozoic.

It was pointed out earlier by Buchholz (2) that embryologically section *Stachycarpus* in part (now section *Afrocarpus*) and *Nageia* may have the most primitive type of embryogeny. On this basis *Nageia* and *Afrocarpus* would seem to be among the more primitive sections. Furthermore the leaves of section *Nageia* have very much in common with another genus, *Agathis*, of which we have examined a number of species. *Agathis* differs primarily in having the resin canals situated between the vascular bundles rather than beneath them, next to the phloem. Indeed the leaves of sect. *Nageia* and *Agathis* also have much in common with those of certain fossil Cordaitales. Regardless of the precise point of origin in evolution, it appears unlikely from morphological considerations that *Polypodiopsis*, *Sundacarpus*, or *Eupodocarpus* are primitive.

Stachycarpus has been singled out by Wilde (15) as possessing a primitive type of grouping of strobili. This may be correct so far as it concerns the arrangement of pollen cones and seed cones, but not necessarily the origin of the strobilar structure itself. There is still a gap between the specialized branch, bearing cones, and the cone borne terminally at the end of a lateral unspecialized branch. There is the question, therefore, whether the condition of *Dacrycarpus* stands at the end of a reduction series from a specialized branch bearing clustered cones, or whether this solitary terminal cone on an unspecialized branch may not represent a more primitive condition, before specialized branches arose. Wilde treats sect. *Dacrycarpus* as if it were derived from sect. *Stachycarpus*. As we have observed in numerous specimens belonging to sect. *Dacrycarpus*, we are inclined to agree with Wasscher's description of these cones, namely, that they are terminal on short lateral unspecialized twigs in which the leaves of these twigs gradually merge into the little-different microsporophylls.

It may be pointed out that Wilde's (15) arrangement of female cones in the entire series for the genus is realized fully within the sect. *Stachycarpus*, even as we have restricted this category. Here, as she points out, *Podocarpus andinus* and *P. spicatus* show the most primitive condition among living forms, whereas, *P. montanus*, in which only a single ovule (sometimes two) remains to form the seed in a terminal position, represents an end member as extreme as any of the others which she cites. In *P. montanus*, of which we are including views of the female fertile branches (figs. 19, 24, 27), not only is the foliage that clothes this member composed entirely of normal leaves, but even the bract subtending the terminal ovule has become enlarged and leaf-like.

Among the sections, our choice of the most primitive has narrowed down to one of three: *Microcarpus*, *Dacrycarpus* and *Nageia*. All of the others save *Afrocarpus* may be excluded. These three sections are the ones about which least is known morphologically — not even the taxonomic characters are fully understood.

Our order of numbering the sections therefore has little significance. Among the three most primitive we are retaining the order given by Pilger in 1903 (12), very largely as a matter of convenience.

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